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A Laboratory Study of Spatial Organization in the Crab *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosiidae)

PATRICK J. SCHEMBRI†

University Marine Biological Station, Millport, Isle of Cumbrae, Scotland KA28 0EG

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In the laboratory, the spatial distribution of *Ebalia tuberosa* on a homogeneous substratum over a 20 day period was mainly random and was not affected by the initial distribution pattern. Population density and population sex-structure similarly had no effect. At low population densities no sexual difference in home range area was found but at high density male home range area was significantly larger than female home range area. There was little overlap in home range between individuals at low population densities but as density increased so did male–male overlap. Female–female and male–female overlap first increased and then decreased. Crowding suppressed female activity. At high population densities, females, and to a lesser extent, males, appeared to restrict their movements to a small area from which they probably excluded other individuals. At all population densities tested, the majority of individuals tended to move for short distances only and very infrequently. The crabs tended to remain in one spot for long periods especially in the case of females which, at high population densities, became very sedentary.

INTRODUCTION

One important aspect of the behavioural ecology of any non-sessile species is the pattern of movement of each individual over the available area and how this is affected by such factors as the density of conspecifics in the same area and their status (e.g. sex, reproductive condition, etc.). Numerous studies on the small-scale spatial distribution and short-term movement patterns of decapod crustaceans have been carried out, however, in the main these deal with semi-terrestrial and inter-tidal species (e.g. Edwards, 1958; Bovbjerg, 1960; Hockett and Kritzler, 1972; Crane, 1975; Vannini, 1976; Aspey, 1978;

† Present address: Portobello Marine Laboratory, P.O. Box 8, Portobello, New Zealand.

Robertson *et al.*, 1980), possibly because these are more accessible. The majority of similar studies on subtidal decapods are concerned mainly with the spatial distribution of semi-sedentary burrowing species (e.g. Chapman and Rice, 1971; Atkinson, 1974a,b). With few exceptions (Hazlett and Rittschof, 1975; Stachowitsch, 1977) spatial organization and individual movement patterns of subtidal free-ranging species have not been investigated.

Ebalia tuberosa (Pennant, 1777) is a small (carapace length 12–16 mm in adults) leucosiid crab found on subtidal gravelly substrata. During daytime the crabs bury themselves in the substratum. No permanent burrows are constructed (Schembri, 1980), the animals simply embedding themselves in the sediment. Often part of the carapace is left uncovered and the crabs closely resemble the surrounding pebbles (Schembri, 1980). During darkness the crabs emerge and forage for food on the surface of the sediment (Schembri, 1980). The spatial organization of this crab and certain modifying factors were studied in a series of laboratory experiments. Ideally, such an investigation should be carried out in the field, however, because of the difficulty of operating at the depths at which the crabs occur in the study area (*c.* 44 m) this was not possible.

MATERIALS AND METHODS

Crabs were collected by dredging from off Farland Point, Isle of Cumbrae, Scotland. Healthy adult individuals were marked by painting numbers on their dorsal surfaces and were then released in a large aquarium and their movements followed by plotting their positions at regular intervals.

The experimental aquarium consisted of a rectangular stoneware tank (length 100 cm × width 40 cm × depth 40 cm) containing a 1.5 cm deep layer of the crabs' natural substratum on the bottom. This was deep enough to allow the crabs to half-bury in the sediment leaving the identification numbers on the carapaces visible. A slow flow of sea-water (salinity 32°/$_{oo}$) was maintained through the tank. The temperature varied between 5–14°C, depending on season. Except for the short term experiments (see below) the tank was kept under a LD 16:8 cycle with a luminous intensity of ~140 lux at the water surface. A grid (10 × 10 cm squares) made of string was placed just above the water surface and the position of each crab relative to the grid lines was found using a plumbline. Plots of the crabs' position were made once a day between 10.00 and 12.00 h during the light phase of the LD cycle. During the course of the experiments the crabs fed regularly on the sediment surface and no additional food was given. Each crab was used once only.

Long term experiments were designed to study the effect of population density on spatial organization. For these, equal numbers of male and female

crabs were placed at the centre of the aquarium and their movements followed for 20 consecutive days. Population densities of 4, 6, 10 and 20 crabs were tested. To determine the effect of the initial distribution pattern on subsequent spatial distribution, the 20-crab experiment was repeated with a different batch of individuals and with the animals overdispersed at the start.

Short term experiments were designed to study the combined effect of population sex-structure and density on spatial organization. Population densities of 4, 6, 10 and 20 crabs were again used. In one series of experiments all the crabs were males, in another all were females and in a third, equal numbers of both sexes were used. The crabs were placed at the centre of the aquarium and their positions plotted after 72 h from the start, following which the crabs were returned to the centre and the experiment repeated. Three replicate experiments were run for each sex-density combination. Short term experiments were run in constant darkness.

Spatial distribution was analysed by the Clark and Evans nearest neighbour measure (R).† The animals are aggregated if the value of the statistic R is significantly less than 1 and regularly spaced if R is significantly greater than 1 (Clark and Evans, 1954). For the long term experiments, the 20 position records for each individual were replotted on one map. The extreme outermost points on the map were then connected by straight lines to form a polygon which included all other points. This polygon was taken to represent the home range of the crab (Odum and Kuenzler, 1955). The home range area (HR) was measured by a weighing method as described by Kawamichi and Kawamichi (1979). Overlap in home range (OHR) was determined by superimposing the home range maps on each other in pairs and measuring the area of overlap. Partly following Hazlett and Rittschof (1975), the following measures were calculated:

Day-to-day movement (DDM): the linear distance between one position record and that of the following day;

Average day-to-day movement (ADDM): the mean of all DDM for an individual;

Single largest movement (SLM): the single largest DDM for an individual;

Zero movements (ZM): the number of zero valued DDM for an individual;

Male records (MR): the total number of male position records in an individual's home range;

† The author is aware of the Simberloff (1979) correction to the Clark and Evans method, but in the present case the diameter of the crabs is so small (approx. 1.5 cm) compared to the bottom area of the experimental aquarium (4000 cm^2) that the correction appears unwarranted. Simberloff (1979) points out that nearest neighbour analyses assuming points instead of circles are sufficiently accurate for small circles when diameter $< \frac{1}{2}r_e$. In the present case $\frac{1}{2}r_e$ ranged from about 8 cm for the 4-crab experiment to about 3.5 cm for the 20-crab experiment hence a reanalysis of the data using Simberloff's correction would not significantly alter the results reported here.

Female records (FR): the total number of female position records in an individual's home range.

Intraexperimental comparisons between males and females were made by the Mann–Whitney U-test, while interexperimental comparisons were made by the Kruskal–Wallis one-way analysis of variance by ranks, both at the 0.05 significance level and corrected for ties where necessary (Siegel, 1956). The 4-crab and 6-crab results were pooled because individually these were too small for analysis by the Mann–Whitney U-test. Correlations between pairs of parameters were determined using the Pearson product-moment correlation coefficient (r) (Zar, 1974).

RESULTS

Spatial distribution

Values of the Clark and Evans R statistic for the 4-, 6-, 10- and the two 20-crab experiments are plotted in Figures 1 and 2. In all cases the crabs were randomly distributed for the greater part of the time. R values fluctuated less as population density increased. The initial distribution did not seem to have any effect on the long term distribution pattern since, irrespective of whether the crabs were aggregated (Figure 1) or regularly spaced (Figure 2) at the start, they tended towards a random distribution.

The results of the short term distribution experiments are given in Table I. Two-way analysis of variance (Zar, 1974) on these results showed that neither

TABLE I

Values of the Clark and Evans R statistic after 72 hours for different population densities of *E. tuberosa* consisting of (i) males, (ii) females and (iii) equal numbers of males and females. The crabs were placed in an aquarium of bottom area 4000 cm^2 and were aggregated at the start of the experiment; three replicates per batch were run; A—aggregated, D—regularly dispersed, all other values represent a random distribution ($P < 0.05$).

Density	Replicate	Males	Females	Males and females
4	1	0.97	1.18	0.53
	2	1.11	1.29	1.43
	3	1.07	1.11	0.93
6	1	1.52 D	0.41 A	0.97
	2	1.59 D	1.57 D	1.43 D
	3	1.08	1.53 D	1.21
10	1	0.82	0.95	1.23
	2	0.69 A	0.86	1.40 A
	3	0.93	1.06	0.97
20	1	1.20	1.38 D	1.29 D
	2	1.33 D	1.02	1.34 D
	3	1.25 D	1.12	1.12

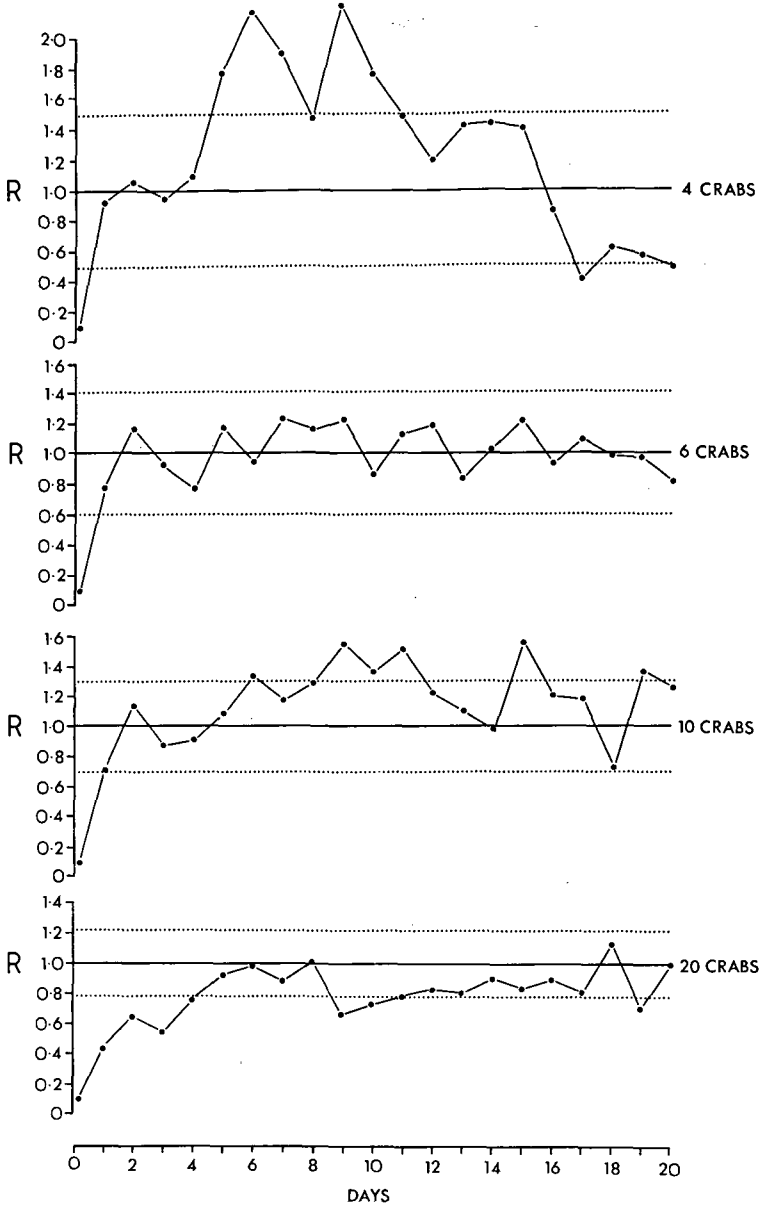

FIGURE 1 The value of the Clark and Evans R statistic on 20 consecutive days for different population densities of *E. tuberosa* consisting of equal numbers of males and females in an aquarium of bottom area, 4000 cm^2. The area between the dotted lines represents the region where the distribution is considered to be random (at $P < 0.05$); values of R falling below the bottom dotted line or above the top dotted line represent aggregated and regularly dispersed distributions respectively.

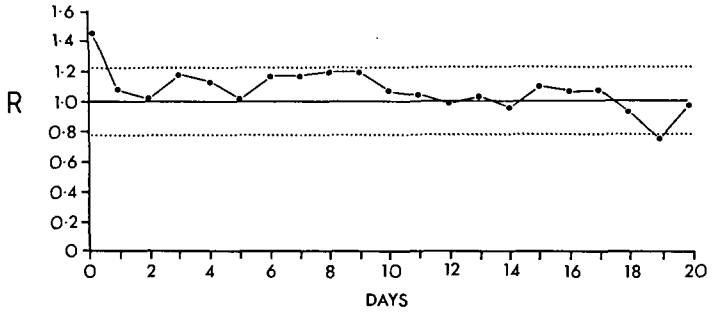

FIGURE 2 Values of the Clark and Evans R statistic on 20 consecutive days for 10 male and 10 female *E. tuberosa* in an aquarium of bottom area 4000 cm^2; the crabs were arranged regularly at the start of the experiment; other details as for Figure 1.

population density nor the sex of the crabs nor these two factors combined had any significant effect (at $P = 0.05$) on the value of R.

Home range and intraspecific interactions

At all population densities except the highest, there is no significant difference in HR between males and females, however in the 20-crab experiment † male HR is significantly greater than female HR (Table II). Unlike male HR, female HR is significantly different at different population densities, the highest mean female HR being in the 10-crab experiment and the lowest in the 20-crab experiment (Table II). HR and ADDM are positively correlated for the 4-, 6- and 10-crab experiments (Table III), indicating that the greater the distance moved, the larger the home range. HR and ADDM are not correlated for either sex in the 20-crab experiment (Table III) implying that when crab density is increased, each crab restricts its movements to a small area.

The mean overlap in home ranges of males with males, females with females and males with females are given in Table IV. These results were not compared statistically but inspection of Table IV indicates that at low population densities (4- and 6-crab experiments) there is little overlap. In the 10- and 20-crab experiments male–male overlap increases but the values of male–male OHR for the 10- and 20-crab experiments are more or less identical (Table IV) showing that crowding does not cause males to overlap with other males in proportion to density. Values of female–female OHR and male–female OHR are highest for the 10-crab experiment but low for the 20-crab experiment. At high population densities, therefore, females overlap more with other females and with males than at lower population densities. Under very crowded

† Unless otherwise stated "20-crab experiment" refers to the 10 male, 10 female experiment in which the crabs were aggregated at the start.

TABLE II

The mean home range area (HR) and the mean number of male (MR) and female (FR) position records included in the home range for different population densities of *E. tuberosa* consisting of equal numbers of males and females; for full explanation see text; numbers in parentheses are standard deviations

	HR (cm^2)		MR		FR	
Density	Males	Females	Males	Females	Males	Females
4	1245.0 (1137.2)	361.0 (7.1)	1.0 (0.0)	10.5 (7.8)	15.5 (2.1)	0.5 (0.7)
6	677.0 (364.9)	310.8 (359.6)	15.7 (8.1)	9.3 (16.2)	11.0 (4.6)	0.3 (0.6)
10	1526.2 (1027.3)	1757.2 (908.9)	32.4 (21.9)	48.2 (21.2)	39.8 (30.2)	31.4 (21.6)
20	1137.4 (334.5)	104.9 (83.6)	94.6 (21.2)	17.3 (11.3)	106.8 (47.3)	26.0 (23.3)

TABLE III

Pearson product-moment correlation coefficients (r) for the relationship between home range area (HR) and average day-to-day movement (ADDM) for the different population densities of *E. tuberosa* tested; for the 10-crab and 20-crab experiments, the correlation coefficients were calculated separately for the two sexes

Density		r	d.f.	P
4		0.963	2	$0.02 < P < 0.05$
6		0.892	4	$0.01 < P < 0.02$
10	Males	0.905	3	$0.02 < P < 0.05$
	Females	0.977	3	$0.002 < P < 0.005$
20	Males	0.435	8	$0.20 < P < 0.50$
	Females	0.578	8	$0.05 < P < 0.10$

conditions, female HR is very much reduced (Table II) with less possibility of overlap with individuals of the same or opposite sex.

An additional measure of interaction between individuals was obtained by counting the number of male and female position records which fell within an individual's home range (Table II). The number of MR in male and female home ranges is not significantly different in the 4-, 6- and 10-crab experiments. Males appear not to be excluded from the home ranges of other males or of females. In the 20-crab experiment a significantly higher number of MR is

TABLE IV

The mean male–male, female–female and male–female overlap in home range (OHR) for different population densities of *E. tuberosa* consisting of equal numbers of males and females; numbers are OHR values in $cm^2 \pm$ standard deviations; figures in parentheses are the number of observations

Density	Male/Male	Female/Female	Male/Female
4	13.23 (1)	3.78 (1)	127.6±119.6 (4)
6	344.1±300.2 (3)	0 (3)	123.6±209.6 (9)
10	676.3±579.2 (10)	967.0±573.4 (10)	1001.0±744.7 (20)
20	678.9±333.2 (45)	13.4±19.7 (45)	64.6±70.7 (100)

TABLE V

The mean average day-to-day movement (ADDM), mean single largest movement (SLM), and mean number of zero movements (ZM) for different population densities of *E. tuberosa* consisting of equal numbers of males and females; for full explanation see text; numbers in parentheses are standard deviations

	ADDM (cm)		SLM (cm)		ZM	
Density	Males	Females	Males	Females	Males	Females
4	10.2 (4.9)	5.6 (1.8)	38.2 (11.4)	21.9 (12.1)	3.0 (1.4)	5.5 (0.7)
6	10.3 (2.3)	8.7 (8.8)	23.9 (18.5)	17.6 (13.4)	4.7 (0.6)	3.7 (4.0)
10	19.9 (12.9)	20.0 (11.0)	57.7 (34.0)	73.1 (22.2)	3.2 (2.3)	4.0 (1.6)
20	13.1 (4.3)	2.7 (0.7)	41.4 (9.7)	12.8 (6.5)	3.0 (2.5)	8.3 (2.4)

included in male home ranges than in female home ranges. The reason for this is probably due to the reduced HR of crowded females. In contrast to MR, significantly more FR occur in male home ranges than in female home ranges at all population densities except the 10-crab experiment. This may show that females avoid other females, at least at low population densities.

Population density and MR are positively correlated for males ($r = 0.998$, d.f. $= 2$, $P = 0.002$) but not for females ($r = 0.187$, d.f. $= 2$, $P > 0.50$) and similarly for FR (males: $r = 0.986$, d.f. $= 2$, $0.01 < P < 0.02$; females: $r = 0.727$, d.f. $= 2$, $0.20 < P < 0.50$). Since male HR is not affected by increasing population density (Table II) and since male activity is similarly not

affected (see below), then the more individuals present, the more MR and FR which occur in male home ranges. Female activity, and consequently, female HR, on the other hand, are reduced at high population densities and this explains the lack of correlation between density and MR and FR for females. MR and FR combined are positively correlated with both HR and ADDM at all population densities except the lowest. This shows that the larger the individual's home range and/or the more active it is, the more conspecifics it encounters.

Movement

The distribution of DDM values is skewed towards zero in all experiments (Figure 3), i.e. the majority of crabs tend not to move very often and then only for short distances. The distribution of DDM values is similar for the two sexes in the 4-, 6- and 10-crab experiments. In the 20-crab experiment, however, there is more spread in male DDM distribution than in that of females. This implies that crowding suppresses female activity, a feature already suggested from analysis of HR data and related parameters. The various measures of activity (ADDM and SLM) and inactivity (ZM) are all consistent with this. ADDM, SLM and ZM of males and females are not significantly different at population densities of 4, 6 and 10 crabs, but ADDM and SLM of males are significantly greater than those of females while ZM of males is significantly less than that of females in the 20-crab experiment (Table V). There is no significant difference in ADDM, SLM and ZM of males in any experiment. This is not the case with females, however, where ADDM and SLM are lowest and ZM is highest in the 20-crab experiment (Table V).

The frequency distribution of contiguous ZM (Figure 4) is particularly interesting in that it reveals that both sexes remain in the same spot for long periods and do not wander during each period of darkness. At low population densities the crabs may remain in the same spot for 1–3 days but as the density increases, the crabs, particularly females, remain in the same spot for longer periods.

DISCUSSION

The distribution of animals in their environment depends both on the nature of the environment and on the animals' behaviour. *E. tuberosa* is substratum specific (Schembri, 1980) and in the study area (The Firth of Clyde) its preferred substratum, silty sand with gravel, occurs only in localized patches (Deegan *et al.*, 1973). Hence, on a large scale, *E. tuberosa* will tend to be aggregated on these patches. Within these patches, however, the distribution

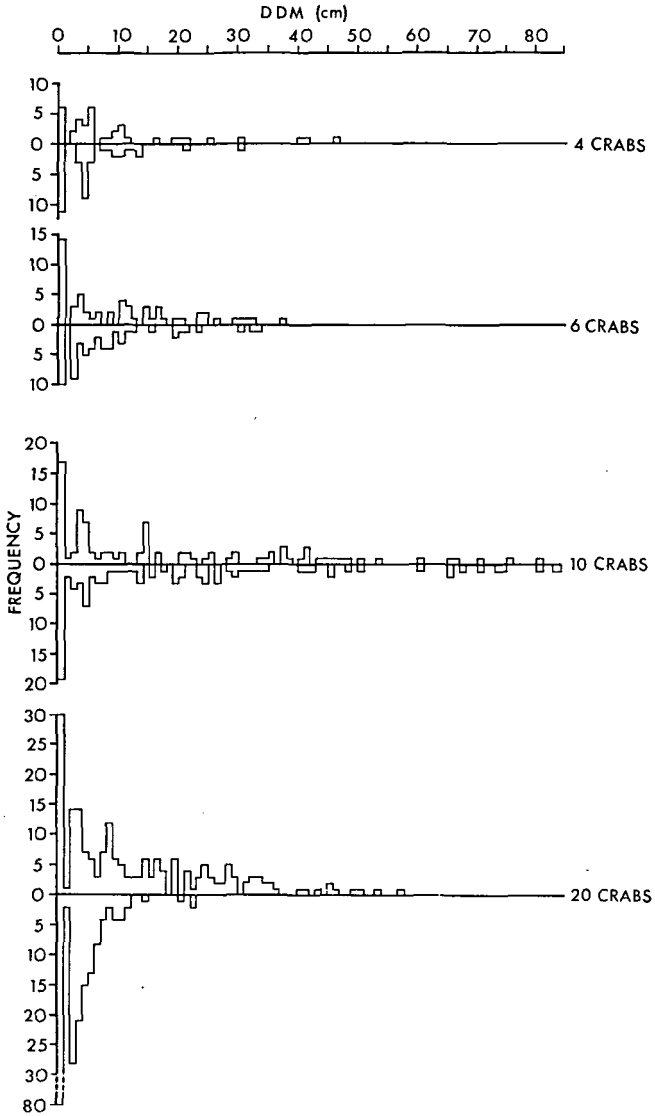

FIGURE 3 Frequency distribution of day-to-day movements (DDM) for the four population densities of *E. tuberosa* tested; upper histograms, males; lower histograms, females.

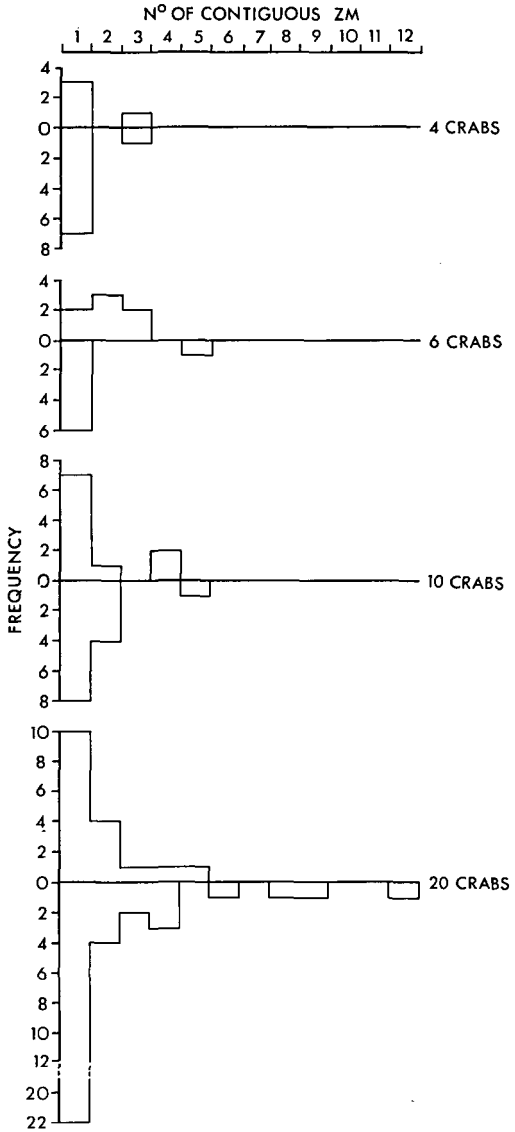

FIGURE 4 Frequency distribution of the number of contiguous zero movements (ZM) for the four population densities of *E. tuberosa* tested; upper histograms, males; lower histograms, females.

pattern will depend primarily on the behaviour of the crabs. The population density of *E. tuberosa* in the Farland Point collection site was estimated to be from 7 to 15 crabs/m^2. These densities are comparable to those used in the 4- and 6-crab experiments.

The experiments described here show that on a homogeneous substratum and over an extended period of time, the distribution is mainly random, irrespective of population density or sex-structure of the population. Far from being static, however, the distribution pattern changes with time. A wider range of R values were observed at the lower population densities than at the higher densities. Presumably, this is because distribution pattern depends partly on the rate at which the individuals in a population meet and as population density decreases, the rate at which individuals come into contact with each other and interact also decreases.

A random spatial distribution may be interpreted behaviourally as indicating that there is lack of response of any one individual to any other (Taylor *et al.*, 1978). Since *E. tuberosa* do not dig permanent burrows (Schembri, 1980) and do not appear to be normally territorial, such an overall random distribution is not entirely unexpected. The crabs obtain the greater portion of their food by foraging on the substratum, though carrion is also occasionally taken (Schembri, 1980). Departure from a random distribution is expected when several individuals attempt to feed on the same piece of carrion as has been observed to happen in laboratory experiments on feeding (Schembri, 1980). Departure from randomness is also expected during the mating season when males court females and possibly compete with each other for mates (Schembri, 1980).

A more detailed analysis of spatial organization indicates that in spite of the implied lack of intraspecific interactions, some interaction must nonetheless be taking place, especially at high population densities when space may become limiting. There is little home range overlap at low population densities, especially female–female overlap, suggesting that the crabs do not trespass on each other's space. The significantly lower number of female position records in female home ranges compared to those in male home ranges at nearly all population densities suggests that females may exclude other females from their ranges. In a field study on the home range and movements of the spider crab *Mithrax spinosissimus*, Hazlett and Rittschof (1975) have similarly found that female crabs exclude other females from their crevices.

Further evidence of intraspecific interactions in *E. tuberosa* is the lack of correlation between home range area and average day-to-day movement at the highest population density in contrast to the positive correlation between these two parameters at lower population densities. This also implies that in crowded conditions movement is restricted to a small area from which the crabs may exclude other individuals. The possibility that crabs actively

exclude other individuals from their spaces is quite likely especially since aggressive interactions involving various threat postures have been observed.

Field studies on *Carcinus maenas* (Edwards, 1958), *Orconectes virilis* (Hazlett *et al.*, 1974) and *Mithrax spinosissimus* (Hazlett and Rittschof, 1975) have shown that in all cases, the males are more active than the females. In *E. tuberosa* female activity was found to be significantly different from that of males only at the highest population density tested, where a high degree of crowding inhibited movement in females but not in males. This inhibition is probably due to a negative interaction (i.e. aggression) between individuals. Crabs confined in a small space interact agonistically when they meet (Schembri, 1980).

Warner (1977) thinks it likely that in most species of fairly slow-moving non-territorial crabs, individuals occur in loosely overlapping home ranges and that they probably do not move far within their ranges from day to day. *E. tuberosa* appears to fit in well in this general picture. At low population densities the crabs do not restrict their movements to any particular portion of the available area, though they tend not to come into close contact with other individuals. At high population densities the crabs range over smaller areas which they probably defend against intrusion by other individuals.

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